DETERMINING THE EFFECTS OF CHANGE IN TEMPERATURE UPON THE LOCOMOTOR MOVEMENTS OF FLY LARVAE

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DISSERTATION

Presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of The Ohio State University

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D. F. MILLER

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PREFACE

The experiments described in the following paper were undertaken primarily for the purpose of justifying my conclusion that many experimenters in the field of insect behavior had neglected to take into account the effects of heat and temperature in their results. As the work progressed I decided to develop it into a dissertation for the partial fulfillment of the requirements for the degree of doctor of philosophy. This seemed justifiable after sufficient work showed that it was possible to isolate, control and accurately measure the effects of the most influential of the environmental factors. Such information is desirable not only as general biological knowledge but especially in the fields of insect physiology and of economic entomology where the success of measures of control often depends upon the basic reactions of the pest to its natural environment.

I wish here to gratefully acknowledge my indebtedness to all those who by their interest and encouragement made it possible to endure the tedium and disappointments which are of necessity the lot of the experimenter.

Columbus, Ohio. D. F. M.
April, 1928.

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DETERMINING THE EFFECTS OF CHANGE IN TEMPERATURE UPON THE LOCOMOTOR MOVEMENTS OF FLY LARVAE [1]

D. F. MILLER
Department of Zoölogy and Entomology, Ohio State University

ELEVEN FIGURES

INTRODUCTION

Light, because of its obvious effects and because of the ease with which it can be manipulated and measured, has occupied the center of attention of most investigators of insect reactions. Much valuable information has been published upon this important subject, but a careful study of this work will, in most cases, show that the experimenter, while in the pursuit of his particular problem, neglected to control or to consider the effect of some other part of the environment. A very noticeable illustration of this is the attempt to measure the effects of light intensities without considering or controlling the temperature. It was partly to show the importance of this that the experiments in this paper were undertaken.

Some carefully done work like that of Patten ('14–'15) is splendid as an illustration of the scientific methods that must be followed for precision work in this field of science. He was, perhaps, not careful enough of the effects of heat. The investigations of Herms ('11) were also well done, but permit of the same criticism, as do those of Mast ('11) in which rate of locomotion of larvae is measured at different light intensities where Nernst glowers are the source of light and no protection from heat or even from reflected light seems to have been made. The simple experiment of Cole ('22) with Drosophila may have suffered from the same effects of heat.

[1] Contribution no. 93 from the Department of Zoölogy and Entomology, the Ohio State University.

since greater light intensity usually means greater heat radiation.

That heat may play an important part in rate of locomotion is self-evident to even the casual observer. It is well known that most flying insects do not fly at low temperatures and that crawling also may be much slower. This has been accurately measured by Shapley ('20) and repeated and verified by Pratt ('25). Perhaps the most exact and carefully

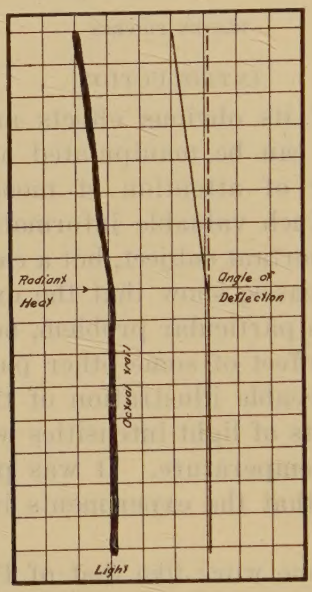


Fig. 1 Trail made by a maggot away from a light source, showing the influence of radiant heat laterally applied and method of calculating the angle of deflection.

calculated work of this nature is that of Crozier and Pilz ('23–'24), Crozier ('24–'25), Crozier and Stier ('25–'26, '28). It has been definitely shown that radiant heat may effect an orientation in much the same way as light (Miller and Gans, '25). I have also shown that when a maggot is retreating from a light source it may be readily deflected from its direct course by radiant heat which reaches it from one side (fig. 1). Wolf and Crozier ('27) obtained similar results with Agriolimax using light and gravity as stimuli.

APPARATUS

In these experiments with blowfly larvae the apparatus was designed to control especially the factors of light, heat, and humidity, as these are known to be important in the reactions of most insects. All work was done in a dark room where the sources of light could be controlled. In order to prevent the reflection of light or the unequal distribution of heat, the apparatus was made light-proof and encased in a water-bath. For the details of construction the reader is referred to figures 2 and 3 and their explanations.

TEMPERATURE AND RATE OF LOCOMOTION

Material

The material used in these experiments was a pure culture of Lucilia sericata Meigen. I started this culture in June, 1927, by catching several flies and placing one each in a milk bottle with a small piece of meat. In a few minutes I found that two of the flies were laying eggs. These two egg masses were then hatched and reared through to the adults. One of the cultures was discarded and the other inbred for four generations before being used. All experiments were performed upon some of the descendants of this one original female.

Maggots for any one experiment were always obtained from eggs laid during the same part of the day, fed upon the same food, and used at the same age of three days (Patten, '16).

Difficulties

The above precautions were far from sufficient to secure uniformity in the material used. Eggs laid by a single female and hatched within twenty minutes of each other would, at the end of three days, show some maggots as much as three times as large as others. The physiological differences so indicated were overcome by selecting for an experiment a number of the largest individuals in a brood. But results of running these through the apparatus showed variations in

time required to travel a distance of 10 cm. at 20°C., ranging from nine seconds up to thirty-five seconds. This further physiological variation had to be eliminated to avoid the use of large numbers of larvae. About three dozen maggots were selected from a culture and run through the apparatus at room temperature. Their record of time was reviewed and from the list were chosen twenty individuals whose time did not vary more than three seconds at the extremes. These were kept in individual vials carefully arranged according to number in a light-proof box.

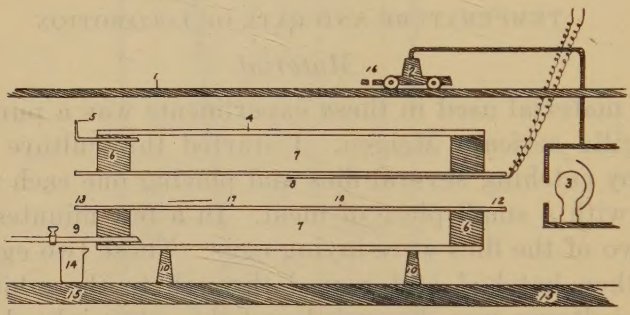


Fig. 2 Diagram giving a lateral sectional view of the apparatus used to measure the effects of temperature changes upon locomotion. *1*, one of the parallel bars of a Leeds and Northrup photometer; *2*, photometer carriage used to regulate the distance of light; *3*, small microscope-stage lamp of 25 watts used to repel maggots through the tube *12; 4*, 50-mm. glass cylinder used as a water jacket for the tube *12–13; 5*, small glass tube as air outlet for water chamber; *6*, rubber stopper; *7*, water chamber used for controlling temperatures; *8*, thermocouple for measuring temperatures in the tube *12–13; 9*, inlet and outlet for changing water in *7; 10*, supports for apparatus; *12–13*, a 15-mm. tube through which the maggots were run during the experiments; *14*, receptacle into which maggots dropped from the end of the tube *13; 15*, framework of wood, supporting apparatus; *16*, small hole in light carriage through which maggots were sighted as they ran the course between *17* and *18; 17–18*, position of the two white threads which determined the 10-cm. course.

Methods

Since exposure to the extremes of high and low temperatures was likely to interfere with accuracy in results, the maggots were divided into two groups of ten each and one group run from room temperature upward and the other

from room temperature down. In making the temperature tests the animals were always run in a definite sequence. A vial was taken from its place in the box and held horizontally between the end of the tube (fig. 2, *no. 12*) and the repelling light (fig. 2, *no. 3*). Thus the retreating maggot was forced from its vial into the testing apparatus. They very often had considerable difficulty in crawling upon the smooth vial, for the maggots themselves were dry and the glass offered little

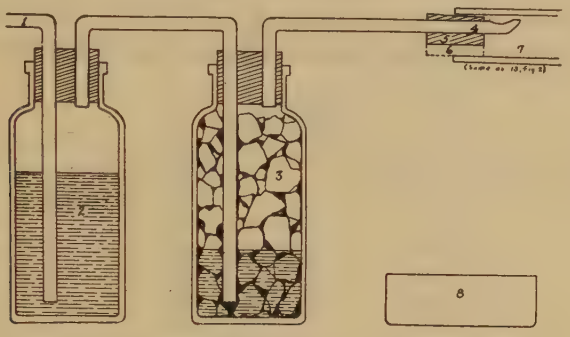


Fig. 3 Humidity apparatus which was used as an attachment to that shown in figure 2 when tests for the effect of humidity upon rate of locomotion were being made. *1*, glass tube connected to air-pressure system (inlet); *2*, one of the solutions of table 2 used to produce a given degree of humidity in the air which passed through it; *3*, same as *2*, except that bottle was filled with pumice to insure thorough contact of air with the regulating chemical; *4*, outlet tube carrying air into the tube, *7*, which is the same as *13* in figure 2; *5*, cork; *6*, hole in cork to permit maggots to leave tube *7*; *7*, experimental tube—*13* in figure 2; *8*, receptacle into which maggots fell when they had run their course.

traction. Mast ('11) says that the amount of moisture on the crawling surface is of great importance. It is my opinion that the amount of moisture is important only in case the surface is quite smooth, as the moisture then gives the maggot more adhesion to the surface upon which it crawls. The apparatus which I used was of such a nature that it rendered impossible the uniform wetting of the path, which in this case was a strip of black-silk ribbon ¼ inch wide. It was almost invariably the case that a maggot which crawled out of its vial with great difficulty proceeded on its way uniformly and

quickly as soon as it was upon the ribbon, which, though smooth and straight, was uneven enough to furnish proper 'footing' for the maggot. This being the case, moisture was neglected, since there is no noticeable physiological effect of the lack of it.

Across this ribbon which served as the path were stuck two white threads 10 cm. apart (fig. 2, *no. 17–18*). These served as markers for timing the rate. The outside of the large tube (fig. 2, *no. 4*), which served as a water-bath, was covered with cardboard, the inner surface of which was dull black. A very narrow slit being left along the upper surface, it was

TABLE 1

NUMBER OF MAGGOTS USED	DISTANCE TRAVELED	AVERAGE TEMPERATURE	AVERAGE TIME
	Cm.	*°C.*	*Seconds*
4	10	2.75	226.6
10	10	7.675	46.77
10	10	10.39	31.26
10	10	15.9	23.99
10	10	22.925	14.08
10	10	30.0	11.93
10	10	35.675	10.30
10	10	40.02	9.75
10	10	44.50	10.80
8	10	51.125	12.00

possible at all times to observe what was taking place in the smaller tube, and any light that might be reflected into the apparatus was symmetrically distributed over the dorsal surface of the animal.

In order to prevent any discrepancy concerning the effect of difference in intensity of light upon the rate of locomotion, a point much disputed in the literature, the light was kept at a constant distance from the animal by making all observations through a small opening in the light carriage (fig. 2, *no. 16*). This hole being kept directly over the maggot as it crawled, the light was at all times the same distance from the maggot. When the posterior end of the maggot was in

contact with the first of the lines, a stop-watch was started and the maggot followed until its posterior end was in contact with the second line and the watch stopped. After this the maggot continued its way and dropped from the apparatus into a receptacle (fig. 2, *no. 14*). The time for the 10-cm. course and the temperature were recorded together. After the data for the ten maggots of one group were re-

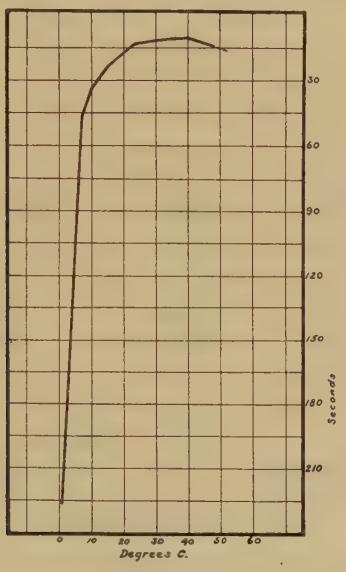


Fig. 4 Graphic representation of the relation between temperature and rate of locomotion based upon the data of table 1.

corded, the water in the water-bath was exchanged for some of different temperature, and the experiment repeated. Table 1 is a summary of these results and shows conclusively the effects of temperature upon rate of locomotion. This is expressed graphically in figure 4.

Humidity

It is quite evident that as the temperature changes took place in the tube the humidity of the air in the tube would also change. This made it necessary to see what effect the

changing atmospheric humidity would have upon the rate of locomotion. To determine the effects of relative humidity apart from change in temperature, it was necessary to be able to change the humidity without changing the temperature. This was accomplished by the ordinary method of pass-

TABLE 2

Solution used	*Approximate per cent of relative humidity*
H_2SO_4	4.00
$CaCl_2$	26.0
NaCl	73.0
H_2O	98.0

TABLE 3

NUMBER OF MAGGOTS	DISTANCE	AVERAGE TEMPERATURE	AVERAGE TIME	RELATIVE HUMIDITY
	Cm.	*°C.*	*Seconds*	
20	10	27.15	12.04	4
20	10	27.20	11.72	26
20	10	27.30	12.14	73
20	10	27.52	11.75	98

	°C.		*Seconds*
Mean temperature,	27.29	Mean time,	11.91
Greatest deviation from the mean,	.22	Greatest deviation,	.23

Per cent of probable error, 1.93

Allowing for corrections in time due to fluctuation in temperature, the per cent of probable error would not exceed 1.5 per cent.

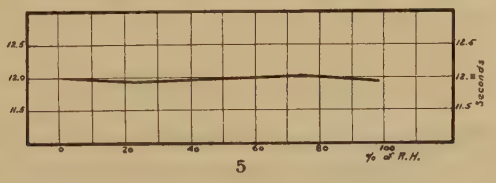
TABLE 4

NUMBER OF MAGGOTS AVERAGED	DISTANCE TRAVELED	TEMPERATURE	AVERAGE NUMBER OF CONTRACTIONS	NUMBER OF CONTRACTIONS PER SECOND
		°C.		
8	10	6.3	29.0	0.627
8	10	10.5	30.125	1.10
8	10	19.1	29.75	1.77
8	10	30.5	30.375	2.39
8	10	38.31	29.615	2.74

Mean number of contractions for each 10 cm.,	29.773
Greatest deviation from the mean,	0.773
Per cent of probable error,	2.9

ing an air current through chemical solutions. The apparatus, in addition to that used in the above experiment, is shown in figure 3. The chemicals and approximate humidities produced are shown in table 2.

The air current was kept constant at all times, and was not strong enough to cause an effect upon the maggots. The



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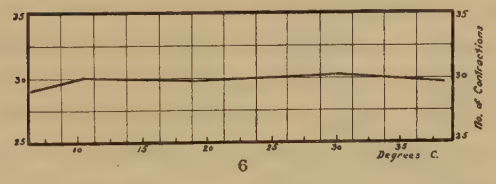

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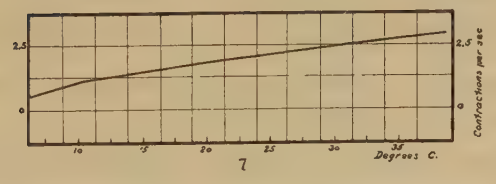

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Fig. 5 Graphic representation of the data contained in table 3, showing that relative atmospheric humidity is not a factor in rate of locomotion.

Fig. 6 This figure shows that the number of contractions required to travel 10 cm. remains constant between 10°C. and 35°C.

Fig. 7 Showing graphically how an increase in temperature from 3°C. to 38°C. causes a continued increase in the rate of contraction.

results obtained are shown in table 3 and in the graph of figure 5, which does not allow for a small correction due to variation in temperature that would produce an even straighter line.

The results of these two experiments indicate the following: 1) that atmospheric humidity is not a significant factor in rate of locomotion; 2) that light, being constant, could not produce differences in rate, and that, therefore, 3) the differ-

ence in rate must be due to the differences in temperature. In what way does change in temperature affect the animal to produce the change in rate?

If, as in vertebrate muscle, both the height and rate of contraction are affected by change in temperature, then the rate of locomotion might be governed by either or both of these conditions. The determination of this point is the subject for the next experiment.

Number of contractions

A group of maggots were selected as in previous experiments and run through the apparatus at temperatures varying from 6.3°C. to 38.3°C. The number of contraction waves passing over while traveling 10 cm. at the various temperatures were counted. The rather unexpected results obtained are shown in table 4 and in the graphs of figure 6 and figure 7.

These results seem to indicate that height of contraction is not affected within the range of temperatures used, while rate of contraction varies directly as the temperature.

GRAPHIC METHOD OF SHOWING THE EFFECTS OF TEMPERATURE UPON CONTRACTION

All the results in the foregoing experiments and those of the last one in particular indicate that a more definite and accurate technique in studying the effect of change in temperature would be of advantage. From most points of view the most satisfactory method would be the graphic one providing the difficulties involved in the manipulation of the apparatus with such an animal as a maggot could be overcome.

Difficulties

The chief problem was that of attaching the animal to the writing lever of the kymograph. Anesthetics were tried in order to quiet the writhings of the maggot while being attached, but these always seemed to leave an abnormal after-effect and frequently killed. Cooling to a low temperature

by placing a number of maggots in a vial surrounded by snow or chipped ice was next tried. After a while the maggots became quiet, usually straight and slightly rigid, which was an ideal condition for handling and left no after-effects.

Passing a fine hook through each end of the maggot and fastening the hooks to the apparatus with threads proved useless, as the puncture immediately released all the body fluid of the animals, which then collapsed. Tying a thread around the ends of the maggot was also unsatisfactory, since this cut off the oxygen supply from the spiracles which are located at the ends of the body. Some maggots with threads tied tightly around the anterior extremity were seen to send waves of contraction from the anterior to the posterior instead of the reverse normal direction.

An attempt was made at using induction shocks after the fashion for vertebrate muscle. The results were useless, since a shock of sufficient strength to produce a contraction seemed to generally cause a tetanus, and no rhythm could be produced. Both normal and decapitated larvae were used.

It seemed that the only satisfactory method was to glue the anterior and posterior ends of the maggot to small strips of paper which could be attached to the apparatus with thread. This still presented some difficulties, but proved efficient when the maggot was properly attached.

Apparatus

With this settled, it was a comparatively simple matter to devise the rest of the apparatus, for details of which the reader is referred to figure 8. Parts not included in the diagram were a standard kymograph and a time clock and signal magnet.

THE MAKING OF RECORDS

General methods

The outside of the apparatus was shielded with black-surfaced cardboard, so that the only light that could enter

the inner chamber which contained the animal had to come through the upper end of the tube (fig. 8, *no. 6*). Since the maggot was always suspended with its head down, the light always reached it from behind. Thus oriented away from the source of the stimulus, the maggot would attempt the

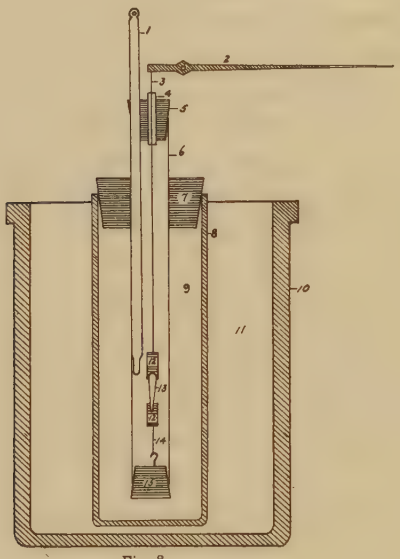

Fig. 8

Fig. 8 A sectional diagram of the apparatus used in connection with the kymograph in obtaining graphic records of the effects of temperature. *1*, thermometer graduated to 0.1°C.; *2*, writing lever; *3*, thread connecting writing lever with the maggot, *13*; *4*, capillary tube permitting thread *3* to pass into apparatus; *5*, stopper; *6*, 15-mm. tube forming experimental chamber; *7*, rubber stopper closing the air chamber *9* in the glass cylinder *8*; *8*, glass cylinder, 50 mm.; *9*, air chamber; *10*, battery jar; *11*, water chamber for producing temperature changes; *12*, small strips of paper to which maggot was glued; *13*, maggot; *14*, thread; *15*, cork containing hook for fastening maggot at one end.

crawling movements of locomotion. Each wave of contraction passing over the larva tends to draw the posterior end down toward the anterior, so that every contraction phase resulted in an upward sweep of the recording lever and each relaxation phase in a downward sweep. Attempts were made at accumulating records upon the following points:

The effects of temperature change upon the rate of contraction. It was not difficult to obtain records to show this effect after a maggot had been properly attached to the apparatus. A time signal was used to facilitate calculation of rate, and

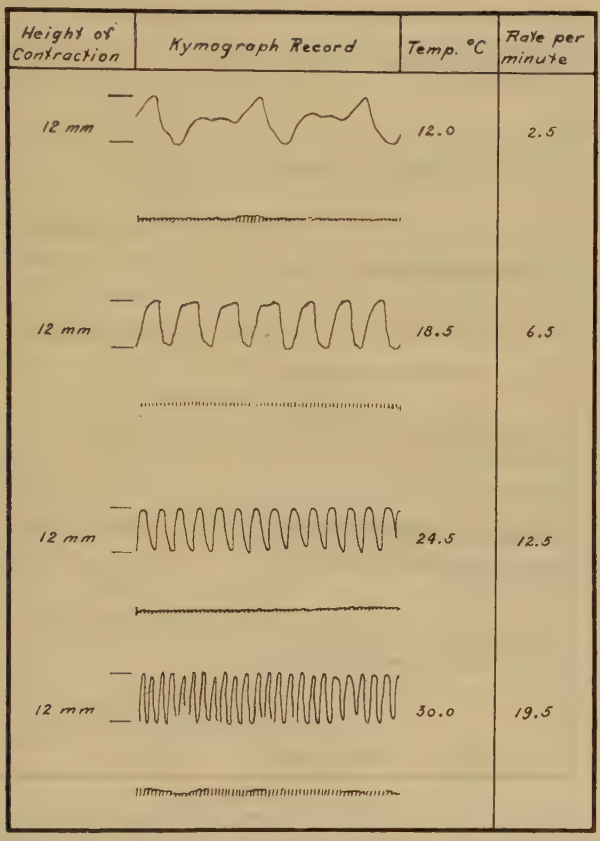

Fig. 9 Kymograph record of one maggot covering a temperature range from 12°C. to 30°C., showing a constant increase in rate of contraction, while the height of contractions remains unchanged.

the results are shown in such records as those given in figure 9, all made by the same maggot. The very evident relation between temperature and frequency of contraction shown by these records directly substantiates the results obtained by counting the contractions in an earlier experiment.

Now, if particular attention be given to the record of figure 10, it may be seen that it gives the activity of a single maggot over a range of temperature from 3.5°C., with no activity, up

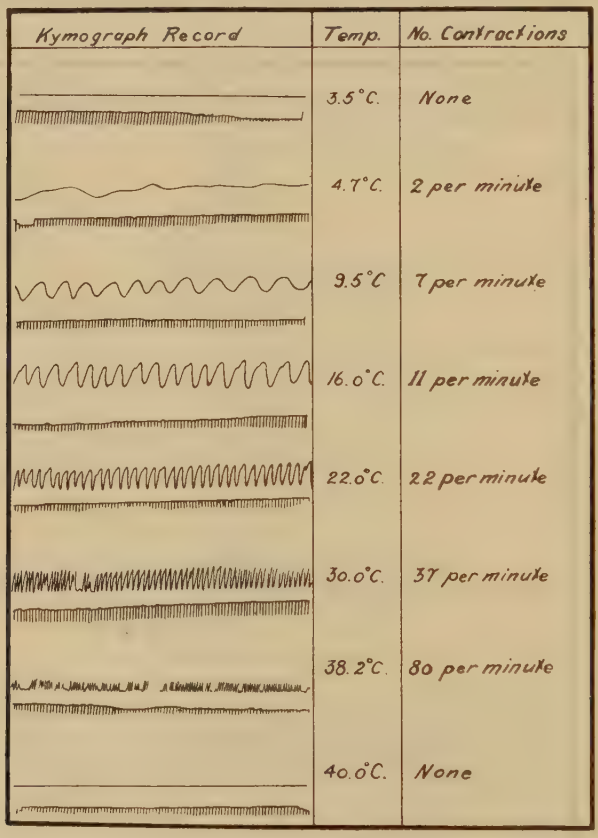

Fig. 10 Kymograph record of one maggot covering a complete activity range of temperatures from 3.5°C. to 40°C., showing the relation of change in temperature to change in rate of contraction and to height of contraction. Note the lack of activity at 3.5°C. and again at 40°C.

to 40°C., with no activity. Between these extremes there is a definite increase in rate with each succeeding rise in temperature.

The effects of temperature upon the height of contraction. By comparing the different parts of the graph of figure 9 it

will be seen that the increases in temperature show the characteristic increases in rate of contraction, while the same increases in temperature cause essentially no increase or decrease in the height of these contractions. All of which corresponds with the general deductions made from the earlier experiments by counting the contractions.

But in this connection figure 10 should be examined again since a much more complete range of temperatures and activities are included in it. This shows that at temperatures below 10°C. the height of contraction is decidedly less than above this point. Above 10°C. there is essentially no change till a point above 30°C. is reached, beyond which there is a constant decrease with further rise in temperature. Therefore, the physiological optimum for height enjoys a wide range of temperature, while rate increases with the temperature.

DISCUSSION

The experimental work described in the preceding pages falls logically into two parts: a group of experiments, largely observational in nature, designed to study the effects of temperature changes upon the locomotor movements of maggots, with complete control over such factors as light, temperature, and humidity; and a somewhat similar group, entirely graphic in nature, designed to substantiate, if possible, those of the first group, as well as to clear up obscure points and to add new information and greater accuracy.

Observational

In the work of Mast, Patten, Cole, and others there is considerable difference in results in their attempts to determine the effects of light intensity upon the rate of locomotion in maggots, and it seems to me that very often these differences might have been accounted for by their failure to properly provide against the effects of temperature, which, I had reason to believe from previous work of my own and from such work as that of Crozier and Stier ('25–'26), to be a very

important factor. The results obtained from the first set of my experiments show clearly enough that there is a very specific relation between the temperature and the rate of locomotion. An analysis of the graph in figure 4 shows these results:

First, the total temperature range of activity is probably from about 2°C. to about 42°C. Below 10°C. there is an excessively rapid drop, and below 2°C. there is rigor due to cold. From 10°C. to a point well over 30°C. there is a much slower increase in rate of locomotion, and above 40°C. there begins a decline in rate, showing that the optimum has been passed. This corresponds to some of Miss Lodge's observations (Lodge, '18) on the orientation of flies to zones of heat from a gas burner where the optimum was from 42°C. to 44°C.

Concerning the effects of relative atmospheric humidity, it may at first seem unusual to find that there were no measurable effects due to the changes even over as wide a range as was used, 4 per cent to 98 per cent. Shelford ('13), Headlee ('17), and others have shown that there is a direct effect of the atmospheric humidity upon the life-history of insects and upon their ecology and their survival. The results of my experiment are not to be taken as a contradiction of this. It does not mean that, if exposed to very low or very high humidities over a longer period, there would be no response or effect upon the condition of the animal, but that the changes in relative humidity within the tube of the apparatus during the experiments did not have any effect upon the rate of locomotion during that time. Therefore, the changes in rate of locomotion must have been due to the changes in temperature.

It remained, therefore, to decide what the effect of temperature was upon the maggot which produced the change in rate. There are three possibilities in this. First, it might, as in vertebrate muscle, cause the height (extent) of the contraction waves to increase as the temperature increased. This would increase the rate of locomotion without increasing the rate of contraction. Secondly, it might increase the rate of con-

traction without increasing the height of the contractions. This would also result in an increased rate of locomotion. Or, thirdly, it might increase both the height of contraction and the rate of contraction.

The data of table 3 and their graphs, figures 6 and 7, show conclusively the effect for the temperatures used. In the first place, there was essentially no change in number of contractions made in traveling a given distance of 10 cm., which shows that there was no appreciable effect of the temperature upon the height of contraction. If the height had changed, the number of contractions necessary to travel a given distance would also have changed. In the second place, these results show that there was a regular and decided increase in rate of contraction which paralleled the increase in temperature. Therefore, the increase in rate of locomotion is primarily a result of the increase in rate of contraction.

Using the data contained in table 1 as a basis for calculations, it is possible to produce a graph by plotting the log mm. per second against the reciprocal of the absolute temperatures. This has been done in figure 11 and shows that there is, for locomotion, a critical thermal increment at approximately 18°C. and another at 35°C., with a possible third at 7.5°C. This latter is, however, very doubtfully established, because of a lack of sufficient data, and may not exist at all.

The graphic-record experiments

While the results obtained in these experiments seem fairly reliable, there were some points lacking in completeness and there was a larger element of possible inaccuracy, due to the fact that much of the data was accumulated by observation and by stop-watch, than was consistent with the best methods for this type of work. So, to complete the information and to provide against possible inaccuracy, the kymograph was resorted to. Of course, not all the above work could be duplicated upon the kymograph, but such vital points as rate of contraction and height of contraction could very readily be. In examining the results of the graphic method, however, one

point must always be kept in mind: in overcoming the friction in the apparatus and in lifting the writing lever against gravity and its drag upon the drum the maggot was performing considerable work, and the conditions were not the same as in locomotion where the maggot moved with little resistance upon a horizontal surface.

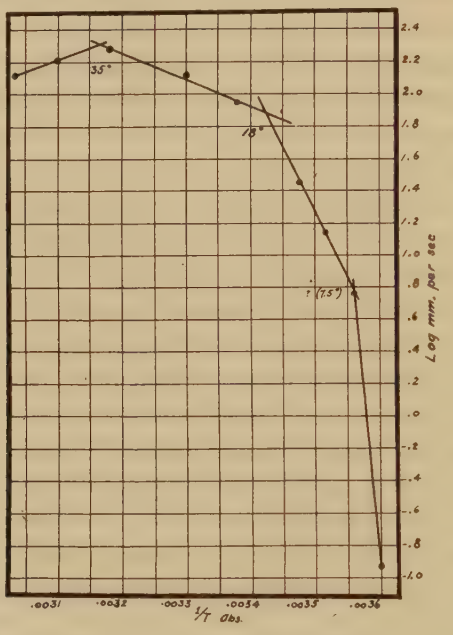

Fig. 11 By plotting the log mm. per second against the reciprocal of the absolute temperature, critical thermal increments are indicated at 35°C., 18°C., and a possible one at 7.5°C., though the last one is questionable.

An examination of figure 10 as an illustration of the results of this method shows several points of interest. First, the record is a complete one for one maggot and covers a temperature range of activity from 3.5°C. to 40°C.. This cuts about two degrees of possible temperature range from both ends of the scale, as compared with figure 4. Here again I feel that this is probably due to the fact that the maggot is manipulating the apparatus instead of actually crawling. Or, there are, no doubt, individual physiological differences suffi-

cient to easily account for this. Furthermore, the values of figure 4 are averages of ten individuals; those of figure 10, from one individual. Secondly, the complete graph of figure 10 shows all phases of activity from no movement at low temperature to no movement at high temperature. Thirdly, the rate of contraction very noticeably increases with each increase in temperature up to the maximum, which makes the rate of contraction a function of temperature (see also fig. 7). Fourthly, the height of contraction does not change materially from about 10°C. to something above 30°C., but does drop off considerably below and above these limits. The optimum range of temperature for height, then, is between the temperatures of 10°C. and, probably, 33°C. This makes the optimum temperature for locomotion the point where the rate of contraction times the height of contraction gives the largest product. Theoretically, the rate of locomotion at any time is:

$$R \times H = L$$

where R equals the rate of contraction and is a function of the temperature and where H is the height of contraction and may vary above and below the optimum.

Furthermore, the information contained in the graphs of figure 10 explain exactly the type of curve obtained in figure 4. There are three parts to this curve. First, a very abrupt and long rise in rate of locomotion from the low limit up to 10°C. Secondly, a fairly regular curve from 10°C. up to near 40°C., and, thirdly, a lesser drop above 40°C. These are explained as follows:

First, below 10°C. both the height and rate of contraction are markedly reduced, so that the rate of locomotion suffers from this double reduction.

Secondly, between 10°C. and a point above 30°C. the height remains unchanged, while there is a regular increase in rate.

Thirdly, above this point there is a decrease in the height of contraction, but the rate of contraction continues to increase. Therefore, there will be a decrease in rate of locomotion only when a point is reached where the loss from height

of contraction is greater than the gain from rate of contraction. In the graph of figure 4 this point is at 40°C., but must be several degrees lower in the kymograph data of figure 10.

SUMMARY

As much of the work of previous writers failed to show clear-cut demarcation between the effects of the various factors of the environment in dealing with the behavior of insects, the foregoing experiments were devised and apparatus constructed to determine the exact effect of changes in temperature upon the locomotion of the blowfly maggot. Variation in intensity of light was obviated by keeping the distance of the animal from the light constant. Humidity was disregarded after experiment showed that it was insignificant as regards locomotion. Temperature changes were controlled and measured. It was found—

1. That the rate of locomotion varied directly as the temperature from the low limit of activity, about 2°C., to about 40°C., and inversely above this point.

2. The rate of contraction increases directly with temperature from 0°C. to 45°C.

3. The number of contraction waves made by a maggot in traveling a given distance, as 10 cm., is a constant between the temperatures 10°C. and about 33°C., which means that the height of contraction of the maggot is the same within this range.

4. Above this temperature optimum and below it the height of contraction decreases. This causes the rate of locomotion to increase up to a point where the loss of height of contraction was greater than the gain from increase of rate of contraction.

5. Kymograph records substantiate these conclusions.

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LITERATURE CITED

COLE, W. H. 1922 Note on the relation between the photic stimulus and the rate of locomotion in drosophila. Science, vol. 55, no. 1434.

CROZIER, W. J. 1924–1925 Critical thermal increment for locomotion of a diploped. Jour. Gen. Physiology, vol. 7, no. 1.

CROZIER, W. J., AND PILZ, G. F. 1923–1924 The locomotion of limax. Jour. Gen. Physiology, vol. 6, no. 6.

CROZIER, W. J., AND STIER, T. B. 1925–1926 Temperature characteristic for locomotor activity in tent caterpillars. Jour. Gen. Physiology, vol. 9, no. 1.

HEADLEE, T. J. 1917 Some facts relative to the influence of atmospheric humidity on insect metabolism. Jour. Econ. Ent. Concord, vol. 10.

HERMS, W. B. 1911 The photic reactions of sarcophagid flies. Jour. Exp. Zoöl., vol. 10.

HOLMES, S. J. 1912 The tropisms and their relation to more complex modes of behavior. Bull. Wis. Nat. Hist. Soc., vol. 10.

LODGE, OLIVE C. 1918 An examination of the sense reactions of flies. Bull. Ent. Res., London, vol. 9.

LOEB, J. 1890 Der Heliotropismus der Tiere und seine Ueberstimmung mit dem Heliotropismus der Pflanzen. Würzburg.

MAST, S. O. 1911 Light and the behavior of organisms. New York.

MILLER, D. F., AND GANS, M. 1925 Some observations on the reactions of the ant Cremastogaster lineolata Say to heat. Jour. Comp. Psychology, vol. 5, no. 3.

MARCHAND, W. 1920 Thermotropism in insects. Ent. News, Phila., vol. 31.

PATTEN, B. M. 1914 A quantitative determination of the orienting reaction of the blowfly larva. Jour. Exp. Zoöl., vol. 17.

———— 1915 An analysis of certain photic reactions with reference to the Weber-Fechner law. Amer. Jour. Physiol., vol. 38.

PRATT, K. C. 1925 Thermokinetics of Cremastogaster lineolata (Say). Jour. Comp. Psych., vol. 5, no. 3.

SHAPLEY, H. 1920 Thermokinetics of Liometropum apiculatum. Proc. Nat. Academy of Science, vol. 6, no. 4.

SHELFORD, V. E. 1913 The reactions of certain animals to gradients of evaporating power of air. Biol. Bull., Woods Hole, vol. 25.

WOLF, E., AND CROZIER, W. J. 1927 Orientation in compound fields of excitation; photic adaptation in phototropism. Jour. Gen. Physiol., vol. 11, no. 1, pp. 7–24.

AUTOBIOGRAPHY

I, David Franklin Miller, was born October 25, 1892, at Greenfield, Ohio. All of my elementary education was obtained in the public schools of Springfield, Ohio. In 1913 I entered Denison University and in 1914 transferred to Wittenberg College, from which institution I received the degree of bachelor of arts in June, 1917.

During 1916-1917 I was an assistant in the zoology laboratory at Wittenberg College and was instructor in botany and zoology for the summer term, 1917, at the same institution. From 1919 to 1922 I was professor of biology at Kingfisher College, Kingfisher, Oklahoma. In 1923-1924 I was an instructor and graduate student in the department of zoology and entomology at the Ohio State University and received the degree of master of arts in June, 1924. Since 1924 I have continued as an instructor and graduate student in zoology and entomology receiving the degree of doctor of philosophy in June, 1928.